THE PREY OF A LITHOPHILOUS CRAB SPIDER
XYSTICUS LOEFFLERI (ARANEAE, THOMISIDAE)

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ABSTRACT. The natural prey of the crab spider *Xysticus loeffleri* Roewer 1955, living under stones, was studied. The percentage of feeding specimens in the population studied was low (1.4–4.6%), and it declined with the beginning of the breeding period. Investigation has shown that *X. loeffleri* is a polyphagous predator. Representatives of twelve arthropod orders were found in its diet. Arachnids (opilionids and spiders) formed the major food component constituting ca. 70% of prey captured. No insect order was present in any considerable percentage. Several worker ants were observed as prey suggesting that *X. loeffleri* is a myrmecophagic spider. Seven incidences of cannibalism were recorded, which all involved predation on adult conspecifics (two males and five females). The length of prey killed by *X. loeffleri* ranged between 1.25 and 15.00 mm (mean 4.68 mm) and constituted from 14.3–187.5% (mean 64.2%) of length of their captors. The most frequently captured prey were small arthropods not exceeding half the size of the spiders.

Keywords: Crab spiders, lithophilic, prey, opilionids, cannibalism

Thomisidae Sundevall 1833 (the true crab spiders) is one of the largest families of spiders including about 2000 species (Coddington & Levi 1991). Most crab spiders are typical cursorial hunters which do not use silk for prey capture; instead, they lie in ambush and wait until prey comes within reach of their long forelimbs and seize it. In many terrestrial communities thomisids are among the dominant invertebrate predators, exerting significant pressure on prey populations (Young & Edwards 1990; Bogya & Mols 1996; Jennings & Cutler 1996; Nyffeler 1999). Despite the common occurrence and predatory significance of crab spiders, few studies have addressed their natural diet. A survey of the spider literature revealed only eleven works that included quantitative data on the prey of Thomisidae (Broekhuysen 1948; Nyffeler & Benz 1979; Morse 1979, 1981, 1983; Ricek 1982; Lubin 1983; Dean et al. 1987; Agnew & Smith 1989; Castanho & Oliveira 1997; Romero & Vasconcellos-Neto 2003). All crab spiders studied in these works inhabit vegetation or ground litter strata. However, many thomisids are known to live under stones. Unlike most cursorial spiders, which use spaces under rocks only as temporary shelters, a variety of thomisid species spend their entire life span here. Physical and microclimatic conditions of this microhabitat differ strongly from those of the surrounding environment (Cloudsley-Thompson 1955). These conditions influence the composition of local invertebrate fauna and thereby the prey available to crab spiders. What is the prey spectrum of the Thomisidae living underneath rocks? How much does it differ from the diets of spiders occurring in other microhabitats?

To answer these questions, I conducted an investigation of the natural prey of the crab spider *Xysticus loeffleri* Roewer 1955, which is among the commonest spiders found under stones in Azerbaijan. The range of this species also includes Turkey, Iran, Middle Asian republics of the former Soviet Union, and Afghanistan (Marusik & Logunov 1994). This is a pronounced lithophilous spider. Over the last several years I observed thousands of individuals of *X. loeffleri* under rocks, while none was seen on the open surface. Like most thomisids, *X. loeffleri* are typical ambushers which spend most of their time sitting immobile on the underside of rocks awaiting prey. These spiders have an annual life cycle (Guseinov, unpubl. data). Adult females are present from September through May, while males are found only in autumn, which ap-

pears to be the mating season (one mating pair was observed). Oviposition usually begins in early spring and continues to the end of May. Females spin hemispherical egg sacs on the underside of rocks which they guard until the young emerge (Guseinov, unpubl. data). Some females were observed guarding a second egg sac near the first empty cocoon. So, *X. loeffleri* seems to be an iteroparous spider.

METHODS

Investigation was carried out at "Bailov Park" in Baku City, Azerbaijan (40°38'N; 49°83'E). This habitat was characterized by pines *Pinus eldaricus* Medw., with an undergrowth of short ephemeral grasses, predominantly of *Calendula persica* C.A.M., *Senecio vernalis* W. & K., *Medicago denticulata* W., *Carduus arabicus* Jaqu., *Hirschfeldia incana* (L.), *Erodium cicutarium* (L.), *Hedypnois cretica* W., *Pterotheca marschalliana* (Rchb.), *Torularia contortuplicata* (Stapf.), *Ornithogalum gossonei* Ten., *Gagea tenuifolia* (Boiss.), *Poa bulbosa* L., *Anisanthea rubens* (L.), *Aegilops biuncialis* Vis., *Hordeum leporinum* Link., *Koeleria phleoides* (Vill.), *Bromopsis* sp. Stones were prevalent on the ground in the study area, with *X. loeffleri* being among the commonest spider species under these stones.

Two consecutive generations of *X. loeffleri* were observed throughout the study period. Spiders of the first generation were studied from 14 February–2 April 1997. Seven surveys were conducted during this time (approximately once a week), which took about 13 hours. Spiders of the second generation were investigated from 9 September 1997–21 May 1998. Thirty-eight surveys were made during this period (on average one per week, but numbers of surveys varied greatly between different months: from one in September and October, when spiders were rare under stones, to six-seven in winter months, which were the peak of spider abundance). Over 56 hours were spent on these surveys.

All surveys were done in daylight hours between 11:00 and 17:00. During surveys, rocks in the study area were overturned and the mouthparts of each individual *X. loeffleri* found were inspected with a 4 power lupe to prevent small prey being overlooked. Stones were chosen randomly, but because the study area was not large (ca. 2500 m²) about 60–

70% of all appropriate sized stones (15–80 cm in diameter) in the study area were examined during each survey. Considering the low mobility of *X. loeffleri* it is highly likely that most spiders were observed repeatedly throughout the study period. Specimens with prey in their chelicerae were placed in separate vials containing 75% ethyl alcohol and brought back to the laboratory for measurement and prey identification. Spiders without prey were left in the field. At the same time, all spiders observed were classified into the following groups: (1) males; (2) solitary females; and (3) females guarding their egg sacs. During every survey, the numbers of spiders with and without prey were counted separately for each of these groups. A few additional prey items were collected during occasional observations in the spring and autumn of 1999 and the spring of 2000. Voucher specimens of *X. loeffleri* and their prey items were deposited at the Institute of Zoology of the Academy of Sciences of Azerbaijan.

A chi square test was used for statistical treatment of the data. Only raw numbers (count data), not proportions, were used for analysis throughout the paper.

RESULTS

Feeding percent.—Only 16 *X. loeffleri*-males were seen throughout the study period (none with prey). Thus, they are omitted in the following consideration and all subsequent references are to females.

Of 2023 female observations made during the study period, only 80 (4.0%) included spiders with prey in their chelicerae. Females of first generation were observed feeding significantly less frequently (6 prey records of 423 observations [1.4%]) than females of second generation (74 prey records of 1600 observations [4.6%]) ($\chi^2 = 8.232$; $df = 1$; $P < 0.001$). Among females of the second generation, spiders observed in winter months (December–February) had the lowest feeding percentages compared to spiders observed in autumn (September–November) and spring (March–May) (Table 1); the difference is significant ($\chi^2 = 4.168$; $df = 1$; $P < 0.05$). Although these winter-feeding females exhibited higher percent of prey capture compared to solitary females of the first generation, the difference is not significant ($\chi^2 = 1.857$; $df = 1$; $P > 0.1$). The percentage of feeding speci-

Table 1.—Monthly variation in the number of spiders observed feeding in second generation female *Xysticus loeffleri*. Females found attending egg sacs are referred to as guarding. Females found without egg sacs are referred to as solitary.

Month	Number of sur- veys	Number of spiders observed			Number of spiders feeding			Percentage of spiders feeding		
		Solitary ♀♀	Guarding ♀♀	Σ	Solitary ♀♀	Guarding ♀♀	Σ	Solitary ♀♀	Guarding ♀♀	Σ
Sep./Oct.	2	25	—	25	2	—	2	8.0	—	8.0
Nov.	3	118	—	118	10	—	10	8.5	—	8.5
Dec.	7	357	—	357	18	—	18	5.0	—	5.0
Jan.	6	324	—	324	10	—	10	3.1	—	3.1
Feb.	7	284	—	284	19	—	19	6.7	—	6.7
Mar.	4	117	—	117	10	—	10	8.5	—	8.5
Apr.	5	27	213	240	2	2	4	7.4	0.9	1.7
May	4	4	131	135	—	1	1	—	0.8	0.7

mens among guarding females of second generation (3 prey records of 344 observations [0.9%]) was significantly lower than among their solitary counterparts (71 prey records of 1256 observations [5.7%]) ($\chi^2 = 12.929$; $df = 1$; $P < 0.001$). Guarding females of first generation were also observed feeding less frequently (none found with prey in 89 observations) than solitary females (6 prey records of 334 observations [1.8%]). However, these data are not sufficient for statistical analysis.

Prey composition.—Altogether 88 prey items were taken from *X. loeffleri*. These were distributed among twelve arthropod orders (Table 2). Arachnids formed the major component in the food of *X. loeffleri* (ca. 70%). Opiliones (Phalangiidae, *Opilio* spp.) was the dominant prey order constituting 40.9% of the total prey. Spiders represented by 10 species from 5 families accounted for 28.4% of all prey caught (Table 3). Thomisidae were most abundant (52% of all spiders killed), followed by Theridiidae Sundevall 1833 (28%), Gnaphosidae Pocock 1898 (12%), and Oecobiidae Blackwall 1862 (8%). Seven conspecifics were captured by *X. loeffleri*, including five females and two males.

Insects comprised 29.5% of all prey records. However, no insect order was present in any considerable percentage (more than 10%). Most abundant were Coleoptera and Hymenoptera, 9% and 8% respectively. Coleoptera consisted of four adult beetles (Carabidae, Curculionidae, Histeridae) and four larvae (Carabidae). Hymenoptera included two parasitic wasps (Ichneumonidae) and five

worker ants (Formicidae) represented by four *Messor denticulatus* Lepeletier and one *Leptothorax* sp. The remaining insects comprised three Hemiptera (Lygaeidae, Nabidae, Pyrrhocoridae), two Thysanura (Machilidae, Lepismatidae), two Collembola (Sminthuridae), one Psocoptera (unidentified), one Homoptera (Aphididae), one Embiomorpha (Oligotomidae: *Haploembia solieri* Ramb.) and one Lepidoptera larvae (Noctuidae). The only centipede captured by *X. loeffleri* was a lithobiid.

Feeding phenology.—The study period covered the entire life span of adult females of the second generation and allowed me to consider seasonal changes in their diet. As seen from Table 4, there are differences in monthly distribution of some prey taxa captured. While most arthropods were primarily caught in winter (December–February), adult beetles and ants were captured only in autumn (September–November) and spring (March–May). This difference becomes more striking if we examine the distribution of prey taxa captured between periods reflecting changes in the temperature regime. Harvestmen and most other arthropods were caught only during the cool season (late autumn–early spring). In contrast, Formicidae and adult Coleoptera were captured only during the warm periods (early autumn and late spring). Spiders were caught throughout the course of the study.

Length of prey.—Eighty-two prey items were measured. Their lengths varied from 1.25–15.00 mm (mean ± SD: 4.68 ± 3.10 mm) and constituted from 14.3–187.5% (64.2

Table 2.—Prey taken by *Xysticus loeffleri* under stones. The larvae of holometabolous insects are marked with an asterisk. Otherwise, holometabolous insects are adults.

Prey taxa	N	%
Insecta		
Collembola		
Sminthuridae	2	2.3
Thysanura		
Machilidae	1	1.1
Lepismatidae	1	1.1
Embiomorpha		
Oligotomidae	1	1.1
Psocoptera		
Unidentified	1	1.1
Homoptera		
Aphididae	1	1.1
Hemiptera		
Lygaeidae	1	1.1
Nabidae	1	1.1
Pyrrhocoridae	1	1.1
Coleoptera		
Carabidae	1	1.1
Carabidae*	4	4.5
Curculionidae	2	2.3
Histeridae	1	1.1
Hymenoptera		
Ichneumonidae	2	2.3
Formicidae	5	5.7
Lepidoptera		
Noctuidae*	1	1.1
Arachnida		
Opiliones		
Phalangiidae	36	40.9
Araneae		
Oecobiidae	2	2.3
Theridiidae	7	8.0
Gnaphosidae	3	3.4
Thomisidae	13	14.8
Chilopoda		
Lithobiomorpha		
Lithobiidae	1	1.1
Total	88	100.0

± 42.2%) of the size of their captors which ranged from 4.75–9.00 mm (7.37 ± 0.95 mm). Size distribution of prey is shown in Fig. 1. The most abundant were small arthropods not exceeding half the size of the spiders, which accounted for 53.7% of the total prey measured. To this group belonged collembolans, an aphid, opilionids, a *Leptothorax* ant, oecobiids, theridiid spiders, and conspecific males. Medium-sized prey (from 50–100% of spider body length) constituted 25.6% and included a psocopteran, curculionid beetles, a lygaeid bug, *Ozyptila*, *Xysticus* sp., gnaphosid spiders, some *Messor* ants and some conspecific females. One fifth of the prey of *X. loeffleri* (20.7%) consisted of large arthropods exceeding the length of their captors. These were thysanurans, an embiomorpha, nabid and pyrrhocorid bugs, carabid beetles, lepidopteran larvae, ichneumonid wasps, a lithobiid centipede, some *Messor* ants and some conspecific females.

DISCUSSION

As is typical of cursorial spiders (Nentwig 1986; Nyffeler et al. 1994), the percentage of feeding specimens in the population of *X. loeffleri* was low. The difference in percentage of feeding specimens between two generations is probably due to the fact that most of the observations of first generation females were made in February and early March, characterized by low temperatures, which probably resulted in inhibited prey activity and, as a consequence, low prey capture by spiders. This assumption is confirmed by the data on seasonal changes in the feeding percent of solitary females of the second generation. Spiders observed in winter months were found feeding significantly less frequently than spiders observed in autumn and spring. In contrast, the difference between these winter-feeding females and solitary females of first generation was not significant. Despite the fact that egg-guarding females occurred only in warm period (late spring), in both years the percentage of feeding specimens among them was lower than among solitary females. Unlike females of an anthophilous thomisid, *Misumena vatia* (Clerck 1757), which build their reproductive nests on leaves, far away from their typical hunting site, flowers (Morse 1985), *X. loeffleri* females construct their egg sacs on the underside of rocks i.e. at the same site where they usually forage. This enables the spiders to catch prey during egg guarding period. However, most thomisids are pronounced ambushers, and the choice of prey-rich foraging sites is an important trait of their

Table 3.—Spiders captured by *Xysticus loeffleri*.

Spider species	N	Sex-age stage
Oecobiidae		
Oecobius maculatus Simon	2	1 submale, 1 female
Theridiidae		
Enoploghatha gemina Bosmans et Van Keer	5	1 male, 3 females, 1 subfemale
Enoplognatha quadripunctata Simon	1	1 female
Theridion melanurum Hahn	1	1 female
Gnaphosidae		
Drassodes lapidosus (Walckenaer)	1	1 juvenile
Haplodrassus dalmatensis (L. Koch)	2	2 juveniles
Thomisidae		
Ozyptila tricoloripes Strand	3	1 submale, 2 females
Xysticus loeffleri Roewer	7	2 males, 5 females
Xysticus sp.	3	3 females

feeding strategy (Morse & Fritz 1982; Beck & Connor 1992). While guarding their eggs, female *X. loeffleri* have no opportunity to change their locations apparently resulting in the declined percent of prey capture compared to solitary females.

Investigation has shown that *X. loeffleri* is a polyphagous predator feeding on a wide range of prey. The predominance of opilionids in its diet is unusual. To my knowledge no spiders are known to feed on harvestmen in any considerable percentage. Thus it might be suspected that *X. loeffleri* specializes on opilionids as an unusual less available prey to spiders. However, this fact is more likely due to the abundance of harvestmen in the environment of *X. loeffleri*. The density of potential prey has not been quantified, but, subjectively, opilionids appeared to be one of the most numerous arthropods inhabiting spaces under stones. Furthermore, some other hunting spiders, such as *Philaeus chrysops* (Poda 1761), *Ozyptila tricoloripes* Strand 1913, *Thanatus kitabensis* Charitonov 1946 and *Drassodes lapidosus* (Walckenaer 1802), were repeatedly seen feeding on harvestmen in this microhabitat. In contrast, only two opilionids were found among about 1500 prey organisms

Table 4.—Monthly distribution of prey taxa captured by second generation female *Xysticus loeffleri*. In round brackets are the mean monthly temperatures (°C). In square brackets are the numbers of spider observations made during a given month.

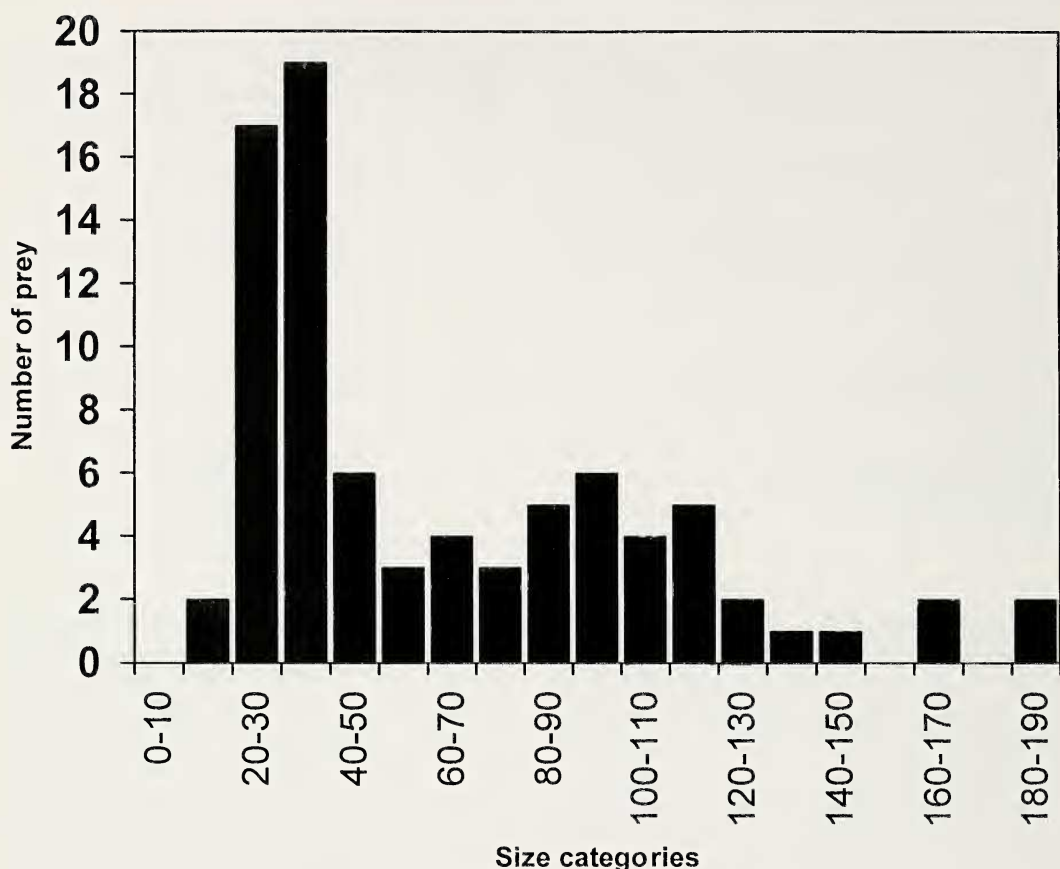| Prey taxa	Sep. (18.8) [8]	Oct. (17.5) [17]	Nov. (10.8) [118]	Dec. (6.2) [357]	Jan. (3.9) [324]	Feb. (3.0) [284]	Mar. (6.6) [117]	Apr. (12.9) [240]	May (14.2) [135]
Opiliones			3	6	6	13	3		
Araneae	1		3	6	2	2	5	1	
Formicidae			1					2	1
Coleoptera (adult)		1	1					1	
Coleoptera (larvae)				3		1			
Ichneumonidae							2		
Hemiptera				1	1				
Homoptera			1						
Thysanura			1			1			
Collembola				2					
Psocoptera						1			
Lepidoptera					1				
Lithobiomorpha						1			

Figure 1.—Distribution of prey in different size categories.

taken from various species of cursorial spiders frequenting other microhabitats (bare ground, herbaceous vegetation, ground litter, bark of trees, stone walls etc.) in the vicinity of Baku City in years 1997–1999 (Guseinov 1999). Thus, opilionids do not seem to be invulnerable prey to cursorial spiders, which probably take them in proportion to their abundance. Which, in turn, apparently depends on the type of microhabitat occupied by the spiders. It is remarkable that some insects (Thysanura, Embiomorpha, Coleoptera larvae) as well as a lithobiid centipede captured by *X. loeffleri* are also characteristic inhabitants of spaces under rocks, but usually lacking among the prey of spiders from other microhabitats (Bristowe 1941; Nentwig 1987; Nyffeler 1999). On the other hand, winged insects (especially Diptera), constituting a substantial part of the food of most cursorial spiders (Nentwig 1986; Guseinov 1997), are almost entirely missing in the diet of *X. loeffleri*. The

tight, constricted spaces under rocks are not favorable environment for winged insects and, as a consequence, crawling arthropods prevail among the prey of *X. loeffleri*.

The high proportion of spiders in the diet of *X. loeffleri* is also probably due to their abundance in its habitat. Many spiders are known to occur under stones and during the cool season their number may even increase in this microhabitat. Although *X. loeffleri* captured mainly cursorial spiders, several individuals of the family Theridiidae most of which are typical web builders were also eaten. The webs of spiders serve not only for prey capture, but are also as efficient defensive devices. Thus only a small minority of spiders are able to invade alien webs and prey upon their residents (Jackson 1992). Most theridiids spin large three-dimensional space-webs. However, the habits of theridiids captured by *X. loeffleri* are apparently different from this common pattern of life style. These spiders were fre-

quently found on the underside of rocks without any silk or with several short threads laid down over the substrate. Therefore, they do not appear to be a more "difficult" prey for predators than typical cursorial spiders.

Xysticus loeffleri is a cannibalistic spider with conspecifics constituting 8% of its prey. Such a high rate of cannibalism is unusual for crab spiders which generally do not hunt conspecifics (Bristowe 1941; Broekhuysen 1948; Morse 1981, 1983; Ricek 1982), but similar to rates of cannibalism of other cursorial spiders from families Salticidae Blackwall 1841 (Jackson 1977), Lycosidae Sundevall 1833 (Schaefer 1974; Framenau et al. 1996), Oxyopidae Thorell 1870 (Turner 1979; Nyffeler et al. 1987a, 1987b, 1992) and Sparassidae Bertkau 1872 (Henschel 1994). Moreover, it should be emphasized that most conspecifics killed by *X. loeffleri* were mature females (71.4%), with size comparable to that of their captors, whereas in cannibalistic lycosid spiders larger individuals usually catch smaller ones (Edgar 1969; Hallander 1970; Yeargan 1975). But such a situation is excluded in the case of *X. loeffleri* because the population consisted of individuals of the same age (Guseinov, unpubl. data).

Despite the fact that worker ants are not acceptable prey to most cursorial spiders (Nentwig 1986), they were found in the diet of *X. loeffleri*, though in low proportion (5%). At the same time, it is known that worker ants compose a considerable portion (30–35%) of the food of some species of the genus *Xysticus* (Nyffeler & Benz 1979; Guseinov 1997). It should be clarified, therefore, whether *X. loeffleri* is a poor predator of ants or if ants are simply underrepresented in the species' habitat. Some data correspond to the second assumption. All ants were caught in early autumn and late spring. Yet, the number of prey records at that time was significantly lower than that in the cool season because the frequency of surveys conducted was low in early autumn and most females had oviposited in late spring resulting in a low prey capture among those females. Thus one can suppose that if the number of prey records in warm periods was greater, then the proportion of observations of ants in the diet of *X. loeffleri* might be larger.

Although small arthropods predominated in the diet of *X. loeffleri*, it does not signify that spiders prefer prey of this size category. This fact is more likely due to the abundance of small prey in the spiders' habitat, since the dominant prey type, opilionids, consisted primarily of small specimens. Probably the appropriate prey size range for *X. loeffleri* is within 20–120% of spiders' body size, since larger or smaller organisms were rare in its diet (see Fig. 1).

Earlier students of crab spiders have pointed out that thomisids often catch very large prey (Lovell 1915; Hobby 1931, 1940; Turner 1946). In feeding expiriments, most cursorial spiders preferred prey not exceeding their own size, whereas the crab spiders, *Xysticus cristatus* (Clerck 1757), readily accepted insects two times larger than themselves (Nentwig & Wissel 1986). Although *X. loeffleri* sometimes captured very large arthropods, most of its prey (ca. 80%) were not exceeding spider length. This is similar to prey size spectra of "typical" cursorial hunters (Salticidae, Lycosidae, Oxyopidae, Sparassidae) (Nentwig & Wissel 1986; Hayes & Lockley 1990; Nyffeler et al. 1992; Henschel 1994), but in striking contrast to flower-dwelling Thomisidae, which commonly feed on prey significantly larger than themselves (Nentwig & Wissel 1986; Guseinov 1999). Experimental investigation is required to clarify whether this difference is due to the difference in size of prey available on flowers and under stones or anthophilous crab spiders are superior toward *X. loeffleri* in catching large prey.

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